Journal of Research on the Lepidoptera 12(4):181-196, 1973

1160 W. Orange Grove Ave., Arcadia, California 91006, U.S.A.

ADULT BEHAVIOR AND POPULATION BIOLOGY OF TWO SKIPPERS (HESPERIIDAE) MATING IN CONTRASTING TOPOGRAPHIC SITES

JAMES A. SCOTT

60 Estes Street, Lakewood, Colorado 80226

Abstract. *Hesperia pahaska* mates on ridgetops and hilltops, whereas the closely related species *Ochlodes snowi* mates in gullies, so that there is little interference between the two. Other behaviors are almost identical in the two species: the method of mate-location in which males sit at characteristic sites and dart out at passing objects in search of females, the time of day of mating, courtship, the rejection dance of unreceptive females, population movements which are fairly large, lifespan, feeding behavior, oviposition, and basking behavior. Interference between species occurs because perching males investigate individuals of related species and numerous interspecific courtships were observed, but is minimized by separate mating locations. The location of mating may not evolve due to interference, but probably evolves in the topographic sites most frequent in the range of a species.

INTRODUCTION

It has generally been assumed that most butterflies mate throughout their habitat. This paper provides evidence that closely related species can mate in very different topographic situations, resulting in little interference between species. Two species were chosen for study: *Hesperia pahaska* Leussler and *Ochlodes snowi* Edwards. They are sympatric at the *Ochlodes* study site and elsewhere at the upper elevational limits of *H. pahaska.* Additional data is presented on two other sympatric species of *Hesperia* which mate in gullies and small plateaus, which show little interference with the sympatric *Hesperia pahaska.* Both species are perching species; perching behavior is defined as a mate-locating system in which males sit at characteristic sites and dart out at passing objects in search of females. It is the opposite of patrolling behavior, in which males fly almost continuously in search of females.

All times are given as 24-hour standard time. I thank Jerry A. Powell for criticizing the manuscript.

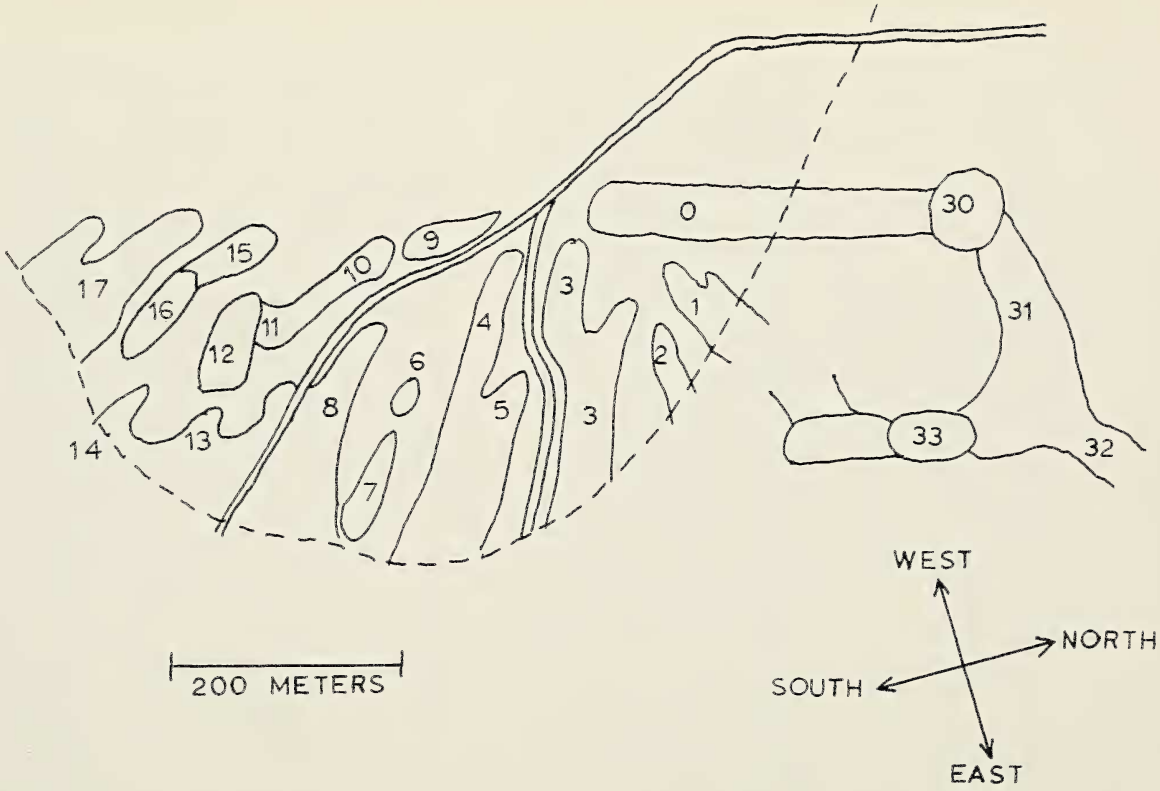

Fig. 1.—Map of the study site of *Hesperia pahaska*. Numbers are area designations; lines outline hills and ridges; double lines are dirt roads. Dashed line is the boundary of the Dry Union Formation (an easily eroded lake deposit) to the west, and metavolcanic gneiss to the east.

METHODS

Marks-A-Lot brand markers were used to give each individual a different number using the method of Ehrlich & Davidson 1960).

A new method of analysis of population movements is used that allows direct comparison between the sexes and between species, determination of change of movements with age, and separation of the velocity and distance aspects of movements. The capture points for an individual are plotted on a xeroxed map of the study site, one map per recaptured individual. The following are determined for each individual:

d_i t_i — distance in m and time in days between the i'th and (i+1) th captures

D — sum of all d's of an individual (total distance)

R — distance in m between the two farthest capture points (range)

T — days between first and last capture

$V = D/T$ (total velocity)

$v_i = d_i/t_i$ (velocity)

Means of the above parameters for all individuals of a sex are computed. Midpoint age is the age midway between two successive captures of an individual after calling the first capture day 0. It was calculated without a correction for worn individuals since all the individuals were in fresh wing condition when first marked. Correlations between the above movement parameters and age determine whether movement changes with age.

Population size, survival rates, and number of new insects per day were found from mark-recapture data using the method of Jolly (1966). In setting up the initial table for the Jolly method, each individual is entered into the table one time less than the number of captures. For example, an individual captured on days 2, 6, 11, and 13 is entered three times, at positions 2-6, 6-11, and 11-13.

Hesperia pahaska (Hesperiinae)

This species was studied in June of 1969 and 1970 at low hills in Chaffee County, Colorado, SW¼ sec. 14 and NW¼ sec. 23, T. 49 N., R. 9E. (fig. 1). *H. pahaska* is found slightly more commonly on the gneiss areas of Fig. 1 but is present everywhere.

Mate-locating behavior. Males perch on stones and other objects from 0700 to as late as 1730, usually from 0730 to 1630. Almost all perching and mating occurs on hilltops and ridgetops, especially hilltops 30, 33, and 12, and sloping ridge 0 (Fig. 1). Perching males sit with wings above the thorax and dart out at passing objects. Males often return to the same spot after an investigative flight. Males are not territorial because movements are fairly large and males often do not return after an investigative flight. Chases between males are more frequent than chases with other species, especially *Amblyscirtes simius* Edwards. There is often "competition" for space, because to avoid interference males must perch more than 3 m from each other. The males not on ridgetops are temporarily at flowers and on hillsides. In one favorable spot on a ridge or hilltop, often 10 males can be collected in an hour as other males move there. At lower densities at other localities competition is also fairly high because males are concentrated on the most favorable hilltops.

Very recently emerged males are less active and old males tend to visit flowers more and perch slightly less than other males.

The few males on hillsides are not as important in mating as the males on hilltops. Males on hillsides do not perch much. They feed and court females on flowers that are usually already mated and unreceptive.

The three species of *Hesperia* at Bear Creek divide up the habitat so that interference between species is minimized. Males of *H. pahaska* perch on ridgetops and hilltops; males of *Hesperia viridis* Edwards perch only on stones or bare spots in the bottom of gullies, especially a small gully southwest of 30 and the gully between 0 and 1. Males of *Hesperia uncas* Edwards perch only on two slight rises in the small 5 m high plateau 3. The larval host of all three is the same, and females of *pahaska* and *viridis* oviposit in the same areas of the hillside of 0, whereas *uncas* females oviposit on the low plateaus like 3 and on the flats around low plateaus. This habitat separation is not restricted to Bear Creek, as I have collected each of the three species at over 50 localities in south-central Colorado, Nevada, Utah, Arizona, and Texas, and everywhere their behavior is the same. In some localities *H. pahaska* perches on the high point of a sloping ridge while *uncas* perches lower down on the ridge. Above 2440 m *viridis* drops out, and below 2440 m normally only *viridis* and *pahaska* occur together, since

uncas requires flatter areas. *H. viridis* is multiple brooded, so normally *H. pahaska* and *viridis* occur together in Colorado only during June and early July. The perching site is probably an evolutionary result of the habitat in most of the range, which is mountain chaparral for *H. pahaska* and great plains for *H. viridis* and *H. uncas*.

Three closely related sympatric skippers have habits similar to the *Hesperia*. *Stinga morrisoni* Edwards perches on hilltops, but only on hilltop 33 and higher hills to the east, perhaps because of lower density in *morrisoni*, while females occur on the same hillsides as *H. pahaska;* it flies slightly earlier than *H. pahaska*. *Yvretta rhesus* Edwards has habits similar to *H. uncas*, but flies about three weeks earlier so is usually gone when *uncas* appears. *Amblyscirtes simius* perches on low hilltops including ridge 0 and hills 1, 2, 3, 12, etc.; this species differs from the previous species in mating only during part of the day, from about 0740 to 1050. Many other perching butterflies there are unrelated enough to cause little interference. Certainly the habitat separation is not the only isolating mechanism, which probably includes olfaction since the courtship is the same in most *Hesperia* species (MacNeill, 1964).

Mating. Two completed courtships were seen. A female flies past the perched male, who flies to within 5 cm. of the female. The female lands, the male may flutter about the female for a short time, then he lands, crawls beside the female and bends the abdomen laterally to copulate. The male sometimes flutters his wings rapidly with moderate amplitude after landing, and the female may flutter her wings silghtly or crawl or fly a short distance. *Hesperia metea* Scudder has similar courtship (Shapiro, 1965). Many courtships of unreceptive *pahaska* females were observed. In these courtships the female upon landing almost always fluttered her wings from vertical to horizontal about 10 times per second. I believe that this is a rejection dance because the females which did this and were later dissected were found to be mated, and because these courtships were never successful. Males often flew away when the female fluttered. The rejection dance inhibits male fluttering; males rarely fluttered behind fluttering females.

The male *Hesperia* has a pouch (stigma) on the front wing full of powder-like material (MacNeill, 1964), which may carry a pheromone. This pheromone may be species-specific because the powder color is different in different species. The male pheromone might be used when the male overtakes the female and flutters his wings.

The virgin female perhaps possesses a pheromone usable within a few feet, because males seem to remain behind virgin females longer than behind mated ones and males relocated several females by approaching from downwind.

Interspecific courtships sometimes occur between the three *Hesperia* species, *Ochlodes snowi*, *Stinga morrisoni*, and *Amblyscirtes simius*. The *Hesperia* female always responds to a male of these species by landing, and then an unreceptive *Hesperia* female usually flutters her wings. The males then often depart.

Females predominantly mate only once, but older females often mate twice and one very worn female was mated three times (table 1). Mated females have a small solid plug in the genital opening, which is evidently ineffective in preventing multiple mating.

Perching, courting, and mating occur at all times of the day in favorable weather. 32 courtships were seen from 0736 to 1644. Copulating pairs were found at 0814, 0830, 1128, 1201, 1312, 1431, and 1544. All matings occurred on the ridge or a hilltop or (twice) within 7 m of a hilltop where they could have flown after a disturbance. Ten virgin females were found from 0812 to 1600, indicating that at least some females wait until the day after emergence to mate. Most of these virgins were found on ridgetops or hilltops where they had flown to seek males. The proportion of females caught on (usually) or within 10 m of a ridgetop or hilltop where perching occurred that were virgin was 32% (13 of 40); the same proportion on hillsides was only 7% (2 of 30). Virgins emerge in early morning (based on laboratory emergence) and apparently remain near the emergence site (usually a hillside) while teneral, then fly to a hilltop to encounter a male on that afternoon or the next day.

Movements. In 1969 the species was marked and captured over the entire area (fig. 1; Table 2). The recaptured males moved 20, 101, 107, 107, 148, 161, 208, 362, and 583 meters, the last two movements in 8 and 10 days respectively. The female moved 20 meters in less than an hour. Several of these individuals crossed the area. The study area was found to be too large for studying dispersal of *Amblyscirtes simius* which was studied concurrently, so in 1970 only areas 0 to 3 and 30 to 34 (fig. 1) were studied. As expected, 1970 distances moved were less than 1969 distances, but velocities were similar. The distances and velocities moved for females are smaller than for males, which may be due to only 8 female recaptures.

Table 1. Relationship of number of matings per female to apparent age (wing condition) of the female in *Hesperia pahaska*.

		WING CONDITION					
		Young				Old	Total
Number	0	10					10
of	1	19	19	13	5	2	58
Spermatophores	2	2	1	1	4		8
	3					1	1

Table 2. Movement data for *Hesperia pahaska*. N = sample size; n = not significant; * = significant at .05; ** = significant at .01; significance of correlations determined by tests of zero correlation.

	1969		1970		1970	
Dispersal Parameter	Males	N	Males	N	Females	N
Number Marked	60		199		53	
Number Recaptured	9		64		8	
Average T (days)	4.44	9	4.03	64	3.87	8
Average ti (days)	3.33	12	2.53	102	3.20	10
Average R (meters)	193.	9	140.	64	101.	8
Average D (meters)	199.	9	174.	64	110.	8
Average di (meters)	149.	12	109.	102	88.	10
Average V (meters per day)	56.	9	59.	64	38.	8
Average vi (meters per day)	51.	12	59.	102	43.	10
Correlation di and ti			+.208*	102		
Partial Correlation di & ti, Age Constant			+.207n	102		
Correlation vi and Age			—.181n	102		
Correlation di and Age			+.032n	102		
Partial Correlation di and Age, ti Constant			—.025n	102		
Correlation ti and Age			+.267**	102		

MacNeill (1964) states: "it is more often females than males which are encountered some distance from a habitable area," which indicates that females disperse more than males. Movements of males which are on ridgetops and hilltops are similar to movements of males on hillsides; many males moved from hillsides to the ridgetop, and vice versa.

There was a small correlation of distance with time between recaptures (table 2). Velocity declined slightly with age, and the time between recaptures increased with age, indicating a slight decrease in dispersal with age.

Population parameters. Males first started emerging about June 9, increased to a peak of about 300 on June 20, then decreased (table 3). The number of new butterflies averaged about 100 per day and gradually decreased. Average survival rate was .741, corresponding to expected lifespan of 3.3 days, using method 1 of Scott (1973). Average survival rate using method 2 (of Scott, 1973) was slightly higher because of day 23: .778 (4.0 days). The potential lifespan is over three times as long. Males lived at least ten (3 males), eleven (2), and twelve days (2). Females lived at least 9 and 10 days. Expected lifespan should be increased because probably many individuals dispersed out of the area.

Feeding. Both sexes often visit flowers. Females usually sit on the ground, bask, visit flowers, and occasionally oviposit. Both sexes visit flowers at all times of day, especially during the hottest part of the day at about 1230 (Fig. 2). Both sexes slightly prefer blue flowers over yellow and white ones, although visits are recorded to all colors. The contrast with *Callophrys siva* Edwards, another butterfly flying with *H. pahaska*, is striking; *C. siva* was common on the flowers of white *Cryptantha jamesi* and yellow *Melilotus officinalis*, and rarely visited other flowers. *H. pahaska* at the study site visited the following species: blue *Penstemon secundiflorus* (94 visits), yellow *Opuntia polyacantha* (43), white *Astragalus drummondi* (20), blue *Cirsium vulgare* (13), white *Cryptantha jamesi* (13) blue-white *Erigeron pumilus* (6), blue *Astragalus bisulcatus* (3), blue *Cleome serrulata* (3), red-blue *Oxytropis lamberti* (3), yellow *Melilotus officinalis* (2), yellow *Hymenopappus filifolius* (2), white *Aster arenosus* (1), white *Asclepias incarnata* (1), yellow *Descurainia sophia* (1), blue *Mirabilis multiflora* (1). Elsewhere they also visited blue *Aster bigelovii*, yellow *Heterotheca villosa*, yellow *Sedum lanceolatum*, yellow *Erysimum asperum*, yellow *Thamnosma montana*.

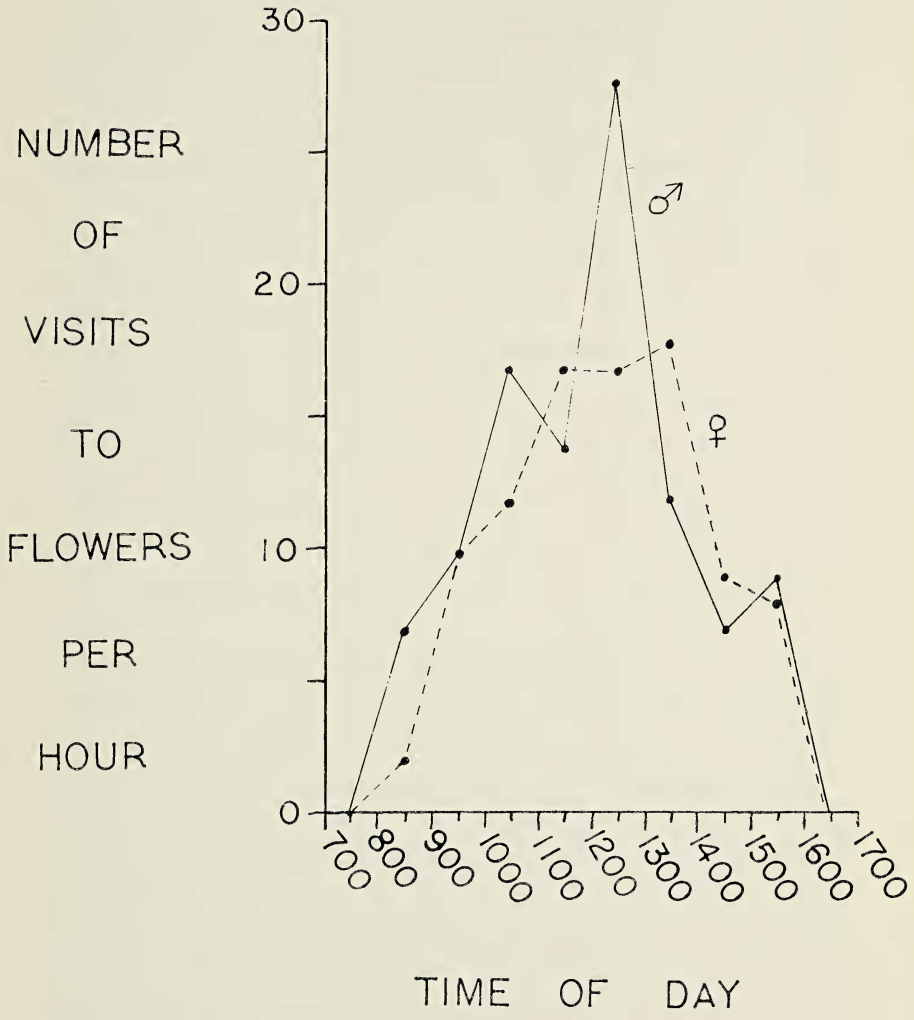

Fig. 2.—Number of visits to flowers at various times of day for both sexes of *Hesperia pahaska*.

Oviposition. Females oviposited on the grass *Bouteloua gracilis,* the probable larval host. An ovipositing female flutters slowly over an area with abundant *Bouteloua,* lands and lays an egg on the lower surface of one of the leaves, usually near the outer edge of a clump. Oviposition was observed throughout the day fram 935 to 1427 with a strong preference for warm, sunny midday hours. Oviposition and other female activity occurred mostly on hillsides, especially the west and southeast slopes of ridge 0. Females seldom oviposit on hilltops, since they are constantly investigated by males there.

Thermoregulation. In cool or cloudy periods both sexes bask by spreading the front wings open about 45° from vertical and hind wings about 70° from vertical. Usually they face away from the sun for maximum insolation, but near midday they face into the wind in the landing position and fail to turn. On hot days (above 80°F) at midday most activity ceases and both sexes seek the shade of a pinon tree or land on its boughs to avoid the hot ground. The study period in 1969 was cold and windy and no individuals were seen to do this, but 1970 was hot in late June and numerous individuals sought shade and trees. Individuals often visit flowers and bask in mild cloudy weather but rarely visit flowers in very hot weather.

Predation. Only one male was caught by a robberfly.

Ochlodes snowi (Hesperiinae)

This species was studied in 1969 in Saguache County, Colorado, near center sec. 22, and NW¼ sec. 23, T. 46 N., R. 8 E., and in 1970 at Rosita, Custer County, Colorado.

Mate-locating behavior. Males perch all day on stones, twigs, or short vegetation in the bottoms of dry narrow gullies which erode during heavy rains but are usually dry. Courtships occur in gullies and at flowers, where females are greatly concentrated. A few males perched in depressions on hillsides and several males perched briefly in the depression between a shrub and the hillside. Perching males fly within about 10 cm of a passing object, then usually return near the last perch. Males investigate objects of the same size range as does *H. pahaska.* In 40 minutes, one male chased 17 other *Ochlodes* males, 9 small flies, 1 2-cm beetle, four brown, black, or blue butterflies less than 3 cm wingspan, and did not chase 5 other butterflies with wingspan 3 cm or greater. When two adjacent males chase each other, they both often rise into the air for 5 meters and rarely up to 30 meters, then separately return to the ground. Males take up a space in the gully about 5 meters long. The species

is usually not abundant, except rarely at flowers, so there is less competition for perching sites than in *H. pahaska*. Most mating undoubtedly occurs in gullies because all females on flowers were unreceptive, and flowers were mostly in glades in stream bottoms near where males perch rather than on hillsides. Males are not territorial because they often do not return to the last perch and move large distances (see below).

Mating. When a female passes by a perched male, or when a female and a male visit the same flower, courtship occurs. If the female flies past, the male approaches within a few cm. This causes the female either to land, or to hover about 3 cm above the ground. If the female hovers, the male hovers also, and moves sideways behind and around the female and now and then moves forward contacting her. Both sexes hover by beating their wings rapidly at wide amplitude. In the one completed courtship, the female landed after the male approached, the male fluttered slightly, landed, and bent his abdomen laterally to copulate. Only two copulating pairs were found, which was surprising since 55 courtships were observed. The male bends his abdomen to attempt joining when the female is on the ground or on a flower. The fluttering of the female on a flower may be the rejection dance of the female, because the male leaves fluttering females after usually 10 seconds or occasionally a minute. The hovering was done usually by mated females. In four courtships in which the female was later found to be virgin, only one of the females hovered while the male fluttered about her; the other three merely sat on the ground with the male behind.

The male has a stigma as in *Hesperia*, which may emit a pheromone. Females may possess a pheromone, because males remained behind virgin unreceptive females for an average of 15 minutes (N = 6). Males remain near females which were mated 1 to 3 times an average of only 7.4 seconds (N = 22).

Two copulating pairs were found in gullies at 916 and 1452. The 55 courtships occurred from 900 to 1535.

Males of all ages, except very recently emerged males, engage in courtship, so males probably can mate many times. Females can mate up to 5 times, and older females are mated an average of 3 times (table 4). Seven virgin females were found from 910 to 1601, indicating that at least some females wait until the day after emergence to mate. Four virgins were found on hillsides, and three were found in gullies. Three of the virgins were visiting flowers, and one was sitting in shade.

Movements. A mark-recapture study was carried out in 1969 at the Saguache County site (Table 5). This area consisted of several gullies separated by ridges and hilltops. Males can move large distances; two males moved 1610 meters to another valley, and a female moved 140 meters. Because this species flies extremely fast, it is not surprising that individuals fly large distances.

Population parameters (Table 6). Average survival rate and corresponding expected lifespan for males was .785 (4.1 days) using method 1 and .736 (3.3 days) using method 2 and ignoring days 16 and 17. These rates should be increased somewhat since many individuals undoubtedly dispersed out of the area. The potential lifespan is much larger; 3 males lived 8 days, and 3 males lived 9 days.

Feeding. Both sexes often feed, especially during the warmest part of the day. Both sexes prefer blue flowers. *O. snowi* in Saguache County visited the following: red-purple *Oxytropis lamberti* (115), blue *Penstemon secundiflorus* (95), blue *Astragalus* sp. (15), blue *Penstemon virgatus* (8), yellow *Hymenopappus filifolius* (4), pink *Geranium caespitosum* (3), blue *Lupinus argenteus* (2), blue *Linum lewisii* (2), red *Gilia texana* (1), white *Cryptantha jamesi* (1), yellow *Potentilla* sp. (1), cream-white *Eriogonus jamesi* (1), pink *Allium* sp. (1). At Rosita they visited a purple legume species (10), *Oxytropia lamberti* (8), *Lupinus argenteus* (2), and pink *Geranium* sp. (1).

Oviposition. Two ovipositions were observed at Rosita, at 1025 and 1035. The female hovers over the most common grass on the west-facing slope where oviposition occurred, *Blepharoneuron tricholepis.* She flies back and forth about 20 cm above the ground and finally lands and oviposits on a leaf at the edge of a clump of this grass. Other females hovered over this grass but did not oviposit.

Thermoregulation. Basking is very similar to that of *H. pahaska.* Upon landing, individuals face uphill, or into the wind, or along a twig. If none of these factors is involved, individuals usually face away from the sun when basking. In cold or cloudy weather, individuals merely sit on the ground with wings closed and may fly very short distances. Early in the morning several males sat on the sunlit east facing side of a gully. Only two males were observed to seek shade because temperature rarely was hot.

Predation. Two males were caught by robberflies at the Saguache County site. The following unusual behavior may lessen predation by vertebrates. After disturbance due to handling for marking, males flew to a nearby tree or shrub and remained there for about 5 minutes. Twenty males did this at all times of day.

DISCUSSION

The behavior of these two species is almost identical except for the location of mating. Perching males investigate objects of many different colors and sizes (Tinbergen et al., 1942; Stride, 1956; Scott, unpublished); in *Hipparchia semele* L. males investigated objects of all colors equally frequently except that white evoked slightly fewer responses (Tinbergen et al., 1942). The wide range of colors and sizes pursued and the frequent interspecific courtships observed mean that considerable interference occurs between species. This interference is minimized by the separation of mating sites where the two species studied are sympatric, as at the *Ochlodes* study-area. The location of mating is correlated with the topographic sites frequent in the range of a species, so interspecific competition may not directly cause evolution of different mating sites. Gullies are frequent in the habitat of *Ochlodes snowi,* but hilltops are less common and are often forested, making them less suitable for perching behavior (but *H. pahaska* males perch there). In the chaparral habitat of *H. pahaska,* hilltops are common, while gullies and small mesas are frequent in the plains habitats of *Hesperia viridis* and *H. uncas.* In many butterfly species males show mate-locating behavior near the larval foodplant, where females are likely to be found, but in *Ochlodes* and *Hesperia* the larval foodplant grasses are widely scattered, so that a strategy of meeting of the sexes in topographic sites is favored. Scott (1968) showed that rare species are much more likely to be hilltopping species, and that hilltopping is a mating mechanism that enables survival at low density by bringing more individuals together for mating than would mate if mating occurred throughout the habitat.

Table 3. *Hesperia pahaska* males, 1970. Population parameters estimated from multiple recapture data using the stochastic model of Jolly, 1966. Alpha—proportion of marked animals; M—total marked population; N—total population; Phi—probability of survival; B—number of new animals joining the population; SE—standard error.

Day	Alpha	M	N + 1.96 SE	Phi + 1.96 SE	B + 1.96 SE
June 9-11	—	—	—	.675 + .589	— —
17	.1143	10.80	94.5 + 103.1	.755 + .536	299.2 + 433.4
18	.0833	30.82	369.8 + 451.1	.906 + .641	—32.2 + 403.1
19	.1860	56.00	301.0 + 256.4	.746 + .544	209.1 + 336.3
20	.1522	65.64	431.3 + 380.2	.499 + .343	—93.3 + 169.2
21	.4211	50.75	120.5 + 89.7	1.198 + .947	210.8 + 310.1
22	.2083	74.00	355.2 + 357.8	.645 + .482	115.8 + 322.4
23	.1724	59.36	344.3 + 315.0	1.322 + 1.184	—132.5 + 383.8
24	.3333	106.25	318.7 + 286.6	.349 + .371	50.4 + 78.7
25	.2545	38.50	151.2 + 115.2	.416 + .411	12.8 + 43.6
26	.2727	16.00	58.7 + 50.8	— —	— —
27-(28, 29, 30)	.0833	—	— —	— —	— —

Table 6. *Ochlodes snowi* males, 1969. Population parameters estimated from multiple recapture data using the stochastic model of Jolly, 1966. Alpha—proportion of marked animals; M—total marked population; N—total population; Phi—probability of survival; B—number of new animals joining the population; SE—standard error.

Day	Alpha	M	N + 1.96 SE	Phi + 1.96 SE	B + 1.96 SE
July 16	—	—	— —	2.833 + 2.560	— —
17	.0625	8.50	136.0 + 294.1	1.489 + 2.268	234.5 + 961.8
18	.0769	33.50	435.5 + 1025.8	.549 + .952	—39.3 + 583.8
19	.1250	25.00	200.0 + 445.4	.964 + 1.352	208.3 + 577.3
21	.0769	30.86	401.1 + 558.7	1.040 + 1.170	521.2 + 429.6
22	.0741	69.50	938.2 + 1571.7	.561 + .743	268.8 + 677.1
23	.0667	53.00	795.0 + 1715.5	.938 + 1.779	—286.5 + 527.7
24	.1316	60.00	456.0 + 844.7	.700 + 1.655	—65.1 + 318.6
25	.1818	42.00	231.0 + 413.5	.381 + .856	—1.7 + 88.2
26	.2105	16.00	76.0 + 126.6	— —	— —
27	.1818	—	— —	— —	— —

Table 4. Number of matings per female versus apparent age (wing condition) in *Ochlodes snowi*.

		WING CONDITION				
		Young			Old	Total
NUMBER	0	7				7
OF	1	19	14	3		36
MATINGS	2		2	7	2	11
PER	3		1	2	1	5
FEMALE	4			4		4
	5				1	1

Table 5. Movement data for *Ochlodes snowi*, 1969. For explanation see Table 2.

Dispersal Parameter	Males	N	Females	N
Number Marked	108		4	
Number Recaptured	23		2	
Average T (days)	3.96	23	0.	2
Average ti (days)	3.14	29	0.	2
Average R (meters)	181.	23	90.	2
Average D (meters)	184.	23	90.	2
Average di (meters)	146.	29	90.	2
Average V (meters per day)	32.	23	90.	2
Average vi (meters per day)	37.	29	90.	2

REFERENCES CITED

EHRLICH, P. R., & S. E. DAVIDSON. 1960. Techniques for capture-recapture studies of Lepidoptera populations. *J. Lepid. Soc.* 14: 227-230.

JOLLY, G. M. 1966. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. *Biometrika* 52: 225-247.

MacNEILL, C. D. 1964. The skippers of the genus *Hesperia* in western North America, with special reference to California (Lepidoptera, Hesperiidae). *Univ. Calif. Publ. Entom.* 35: 1-221.

SCOTT, J. A. 1968. Hilltopping as a mating mechanism to aid the survival of low density species. *J. Res. Lepid.* 7: 191-204.

———. 1973. Convergence of population biology and adult behavior in two sympatric butterflies, *Neominois ridingsii* (Papilionidae, Nymphalidae) and *Amblyscirtes simius* (Hesperioidea, Hesperiidae). *J. Anim. Ecol.* 42:663-672.

SHAPIRO, A. M. 1965. Ecological and behavioral notes on *Hesperia metea* and *Atrytonopsis hianna*. *J. Lepid. Soc.* 19: 215-221.

STRIDE, G. O. 1956. On the courtship behavior of *Hypolimnas misippus* L. (Lepidoptera, Nymphalidae), with notes on the mimetic association with *Danaus chrysippus* L. (Lepidoptera, Danaidae). *British J. Anim. Behav.* 4: 52-68.

TINBERGEN, N., B. D. MEEUSE, L. K. BOEREMA, W. W. VARIOS-SEAU. 1942. Die Balz des Samtfalters, *Eumenis* (*Satyrus*) *semele* (L.). *Z. Tierpsychol.* 5: 182-226.